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THE MALE GENITALIA OF SOME COLIAS SPECIES

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IN MOST FAMILIES OF LEPIDOPTERA the genitalia show such distinctive characteristics that it becomes easy to separate even closely related species. In the family *Pieridae* conditions are different. *Pieris napi* L., *P. bryoniae* Ochs., and *P. ergane* Hbn. are not separable on the basis of their male genitalia, nor are *P. rapae* L. and *P. manni* Mayer (Lorkovic 1928, Drosihn 1933). Similar conditions are present in the genus *Colias*.

Before going into details a general description of the male genitalia of *Colias* will be given (cf. fig. 1). The distal part of the VIIIth tergum is more or less slender, Kusnezov (1915) has called this part the superuncus, Warren (1950) named it the false uncus. At the base of the superuncus the tergum is incompletely sclerotized laterally. The saccus is rounded, sometimes pointed on its sides. The vinculum is long and slender. The tegumen shows a narrow process dorsally, the pseudouncus (Kusnezov 1915). The aedeagus has a long ventral arm.

According to Warren (l.c.) the claspers at their proximal end are restricted to a blunt point, attached to the vinculum. The dorsal edge is said to be drawn upwards, parallel to the vinculum, and the dorsal terminal extremity attached to the tegumen. These statements do not correspond to conditions found in *Protocolias imperialis* (Pl. I, fig. 1). In this species the proximal part of the claspers is rather similar to that of other *Colias* species. The distal part is protracted so that the clasper obtains a shape more or less similar to that of many other Pierids. It may therefore be concluded that the clasper-head with the terminal tooth is the dorsal part of the clasper.

The short pseudouncus and the marked distal lobe of the clasper give to *P. imperialis* a rather isolated position. In some characteristics it comes closer to the genera *Catopsilia* and *Anteos*. In other respects, however, such as the structure of the clasper head, *P. imperialis* is similar to *Colias*, thereby showing the relationship between these genera (cf. Klots 1929 a and b).

In the genus *Colias* the genitalia are rather variable within a species or subspecies, as will be shown below. At the same time the differences between some species are only slight. Therefore a biometrical approach seemed necessary as a complement to the general descriptions of the

genitalia. The modes of measuring and the results are given first as important for the full understanding of the descriptions.

The breadth of the superuncus. The edges of the superuncus in dorsal view may a) converge distally b) run parallely or c) diverge slightly from a narrow part near the base (cf. fig. 2). The breadth was on diverging superunci measured at the narrowest basal point, on others at the corresponding place.

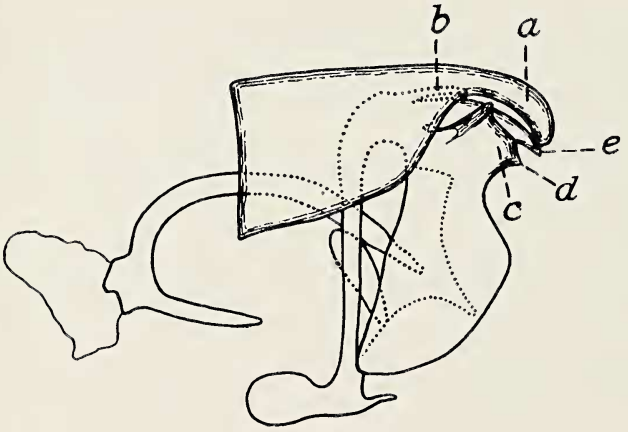

Fig. 1. The male genitalia of a *Colias*. *a* superuncus *b* pseudouncus *c* clasperhead *d* tooth of clasperhead *e* uncus

The size of a certain part of an individual may be influenced by its general size. The breadth of the superuncus has therefore been correlated with a measure of size: the wing length.

All species with genitalia similar to those of the three species previously investigated: *C. hecla, nastes* and *palaeno* are included in fig. 3. Here the breadth of the superuncus is plotted against the wing length in a logarithmic scale. The populations investigated are parted in two groups, the first with a slender superuncus, the second with a broad one. The regression line of the populations with a slender superuncus is:

$$\log \underline{y} = 0.75 \log \underline{x} + 0.68; \ (\underline{r} = 0.72; \ 0.02 > \underline{P} > 0.01).$$

The species along this regression line are both orange with a *hecla*-pattern, yellow with a *hecla*-pattern, and yellow with a *nastes*-pattern. The species in fig. 3 with a broad superuncus are either orange with a *hecla*-pattern or yellow with a *nastes*-pattern. These two types of species can be grouped along two regression lines. Within both groups the correlation is statistically significant.

Orange species:
$\log \underline{y} = 0.80 \log \underline{x} + 0.77$; $(\underline{r} = 0.71$; $0.05 > \underline{P} > 0.02)$.

Yellow species:
$\log \underline{y} = 1.17 \log \underline{x} + 0.30$; $(\underline{r} = 0.81$; $0.05 > \underline{P} > 0.02)$.

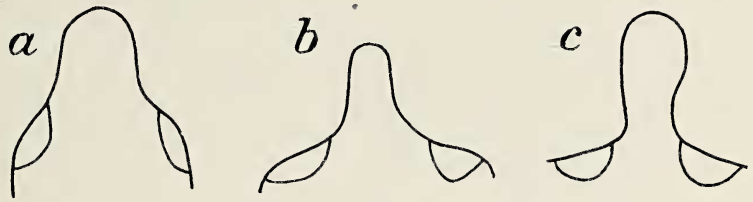

Fig. 2. Differently shaped superunci with semicircular, less sclerotized areas near the base. *a* convergent *b* parallel *c* divergent

The means of the two groups are, however, not significantly separated. An analysis of covariance gives $0.1 > \underline{P} > 0.05$.

The data on which fig. 3 have been based are tabulated in Tables 1 and 2. Among the species shown in these tables *C. nastes* is of special interest. In Scandinavia and in North America but also in Altai and the Sayan Mountains the superuncus is slender. *C. nastes* of Siberia and the Amur Province is intermediate between *nastes* of the Altai and the Sayan Mountains and the closely related, allopatric *C. montium* from S. Kansu. This species forms a transition to *C. cocandica* from Ferghana, the Issykkul, and from the Tianshan. The superuncus-breadth of all Asiatic individuals of *nastes* is plotted against wing length in fig. 4. The populations are grouped along two regression lines, though the correlation in none of the groups is statistically significant (cf. Table 1). An analysis of covariance, however, shows that the means of the two samples (shown in the figure by squares) are significantly different $(0.01 > P > 0.001)$.

In the yellow series of forms there is thus no sharp limit between species with slender and broad superunci. Even within a single population, that from the Amur Province — the variation is so great that it includes superunci typical for *nastes nastes* and others typical for *cocandica* (cf. fig. 4). In the orange series of forms conditions are different as will be treated later. In fig. 5 the superuncus breadth of arctic *C. nastes* and of its sibling in the Alps, *C. phicomone,* is plotted against wing length. The differentiation has proceeded so far that hardly any overlap is present.

The wing length and breadth of the superuncus in some other *Colias* species, less similar to those treated above, are shown in Table 3. In the three pairs at the top of the table the genitalia are so similar that

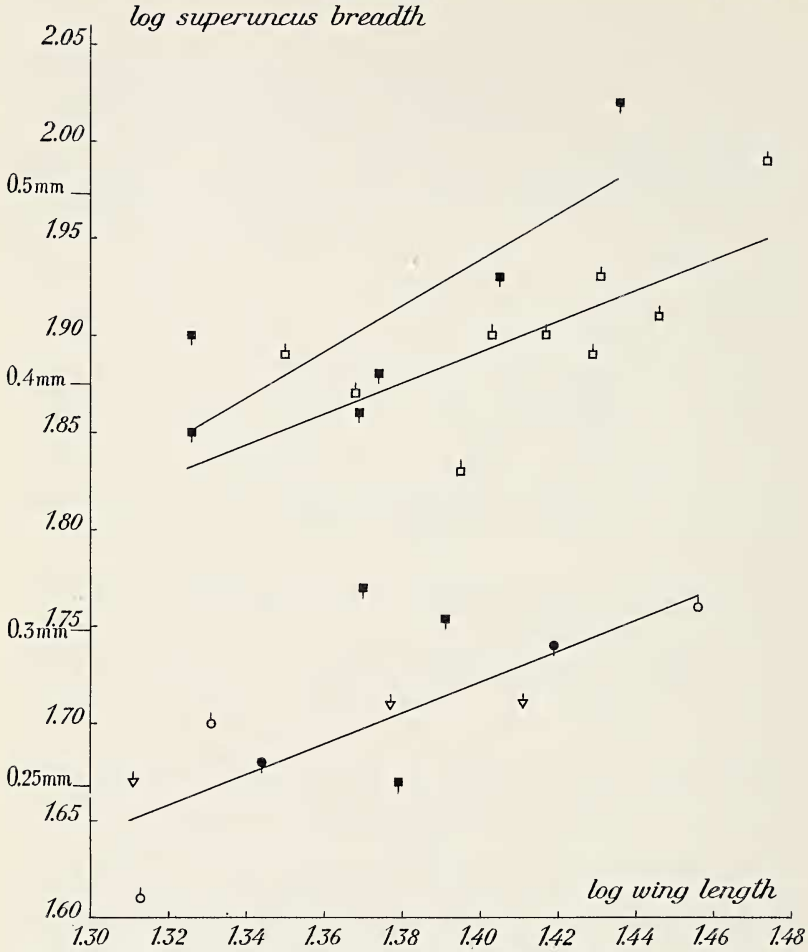

Fig. 3. Superuncus breadth of some *Colias* populations plotted against wing length. Data from Tables 1 and 2.

O Population from N. America or northern Eurasia
□ Population from Central Asia or Central Europe
△ *C. palaeno* and *interior*
rod above=*hecla* patterns
rod below=*nastes* patterns
open mark=orange color
filled mark=yellow color

no constant differences could be found. Warren (1950) states some differences between *C. australis* and *hyale,* a statement which was not confirmed by the specimens investigated.

Two of the species of Table 3, *C. cunninghami* and *P. imperialis,* have an extremely broad superuncus. *C. vautieri,* which otherwise is

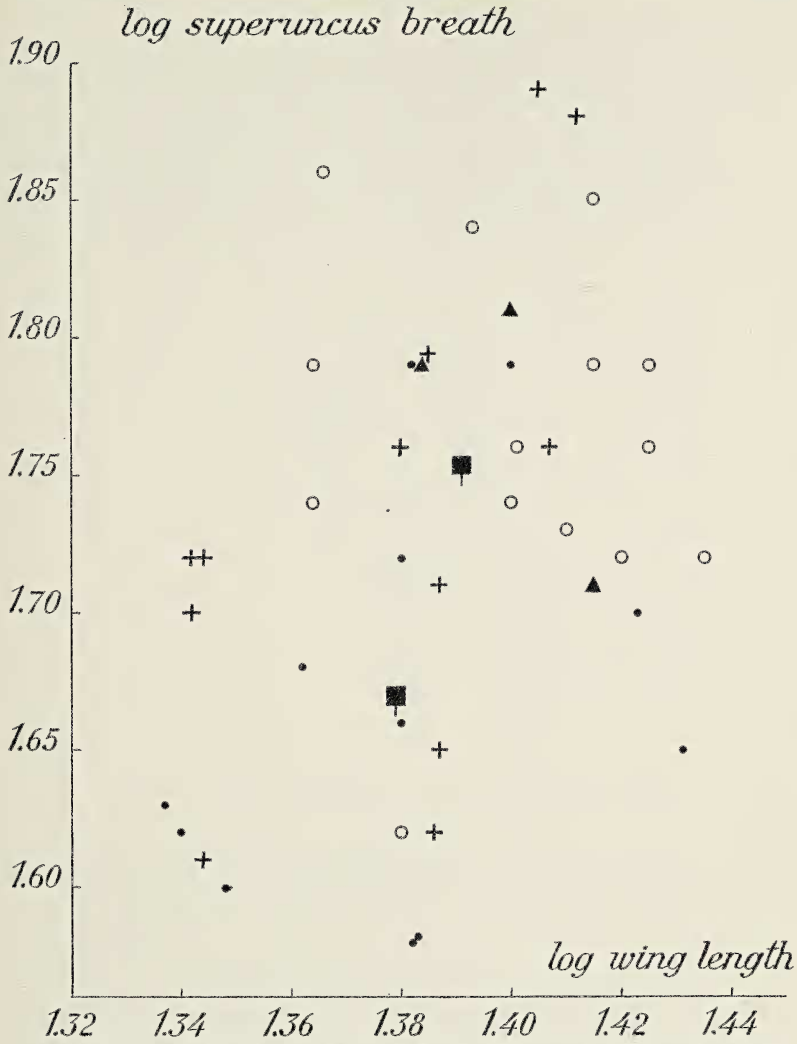

Fig. 4. Superuncus breadth of some Asiatic populations of *C. nastes* plotted against wing length. The lower square represents the mean of the dots, the upper square the mean of the remaining marks.

- • Altai and Sayan Mts.
- O Siberia, Taiga zone
- ▲ Transbaikal
- + Amur Province

rather aberrant, *C. erate,* and *myrmidone* fit well into the group of species with a broad superuncus, listed in Table 2. The remaining four species have a more slender superuncus though *C. hyale* and *australis,* like *C. montium* occupy a somewhat intermediate position.

The form of the superuncus in lateral view. During copulation

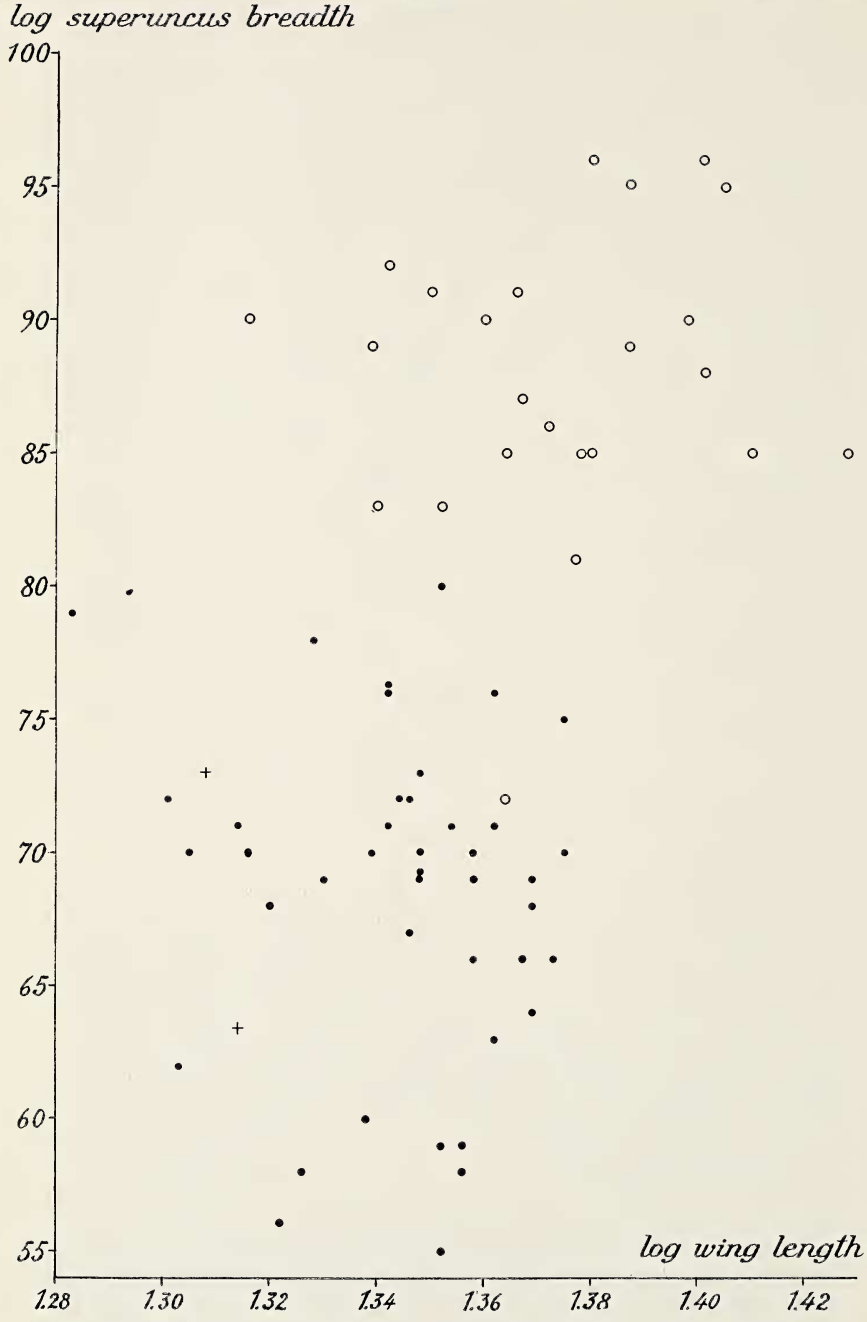

Fig. 5 Superuncus breadth of *C. phicomone* (open circles) and *C. nastes* (filled circles = Scandinavia, + North America) plotted against wing length.

the superuncus together with the uncus is pressed against the body of the female, just as the uncus in the genus *Pieris* according to Lorkovic (1947). To make possible the bending down of the superuncus during copulation a semicircular area laterally on the VIIIth tergit is less sclerotized than the rest (cf. fig. 2). This bending can be stated without studying any copulating pairs. In some specimens the superuncus is broken (cf. fig. 6), in some in addition kept between the two claspers.

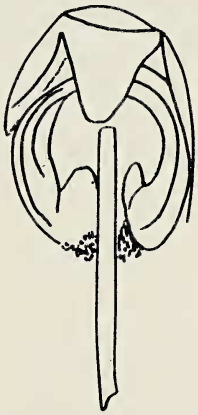

Fig. 6. *Colias interior* with superuncus broken during copulation.

The breadth of the superuncus of such specimens sometimes cannot be measured without maceration. A broken superuncus was found in all species where more than a few specimens were investigated, as shown in Table 4.

Only in very few species the superuncus is a straight process protruding from the VIIIth tergit. Also when unbroken the superuncus usually forms a bow downwards. This bow is present, even in its most pronounced form, in animals which have not copulated, as, for instance, in all the thirty *C. hecia* specimens investigated which in 1952 were caught at the beginning of the flying time on the northern side of the Lake Torne Trask.

To obtain a quantitative estimation of the variation of the form of the superuncus in lateral view, the angle of the distal part of the superuncus to the dorsal edge of the VIIIth tergum was measured. The result of this investigation is shown in Table 4. In general a broad superuncus is only slightly bent downwards while a narrow is bent more. The exceptions are rather few: *C. interior, montium,* and *phicomone.*

Species	n	$M_{\log x}$	$M_{\log y}$	$\underline{r}$	$\underline{P}_{\underline{r}}$	$\underline{b}_{\underline{x}}$
A. Orange species						
C. hecla, Scandinavia	51	1.331	1.70	-0.18	0.3-0.2	-0.74
-"- , Siberia, Dudinska	4	1.355	1.67			
-"- , Baffin, Isl.	2	1.347	1.79			
-"- , Greenland	3	1.362	1.74			
C. hyperborea, N. Siberia	4		1.69			
C. eurytheme, N. America	6	1.456	1.76			
-"- , slightly orange Texas, Houston	6	1.313	1.61			
B. Yellow species						
a. hecla pattern						
C. palaeno, Europe	41	1.411	1.71	0.18	0.3-0.2	0.50
C. palaeno, Siberia	3	1.377	1.71	0.57	0.2-0.1	1.73
C. interior	2	1.311	1.67			
b. nastes pattern						
C. nastes, scandinavia	42	1.344	1.68	-0.09	0.6-0.5	-0.24
-"- , Siberia, Amur area	29	1.391	1.75	0.32	0.1-0.05	0.87
-"- , Altai, Sayan Mts.	12	1.379	1.67	0.35	0.3-0.2	0.86
-"- , N. America	2	1.311	1.68			
C. philodice, N. America	11	1.419	1.74			
C. montium, S. Kansu	9	1.370	1.77			

Table 1. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, and their correlation in some Colias species with a slender superuncus. Logarithmic scale.

C. interior is in this character well separated from its allopatric sibling, *C. palaeno,* in having a rather straight but slender superuncus.

C. montium has a rather slender superuncus which is straight as is that of *cocandica.* In this respect another of the southern species, *C. phicomone,* is intermediate between *nastes* and *cocandica.* The superunus of *phicomone* is, however, rounded and not more or less pointed as it is in all other species with a slender superuncus except *C. interior, aurorina,* and *sagartia.*

By means of the two characteristics, *i.e.* the breadth and the form of the superuncus, it is possible to separate the two species *C. viluiensis* Mén. and *hyperborea* Gr. Gr. which live sympatrically in N.E. Siberia. Of *viluiensis* 7 specimens from the Verchojansk area, Lutsha near Yakutsk, Vilutsk and Vilui have been investigated. The four specimens of *hyperborea* were from Sib. pol., the Lena Valley

Species	n	$M_{log\ x}$	$M_{log\ y}$	Species	n	$M_{log\ x}$	$M_{log\ y}$
Orange species, hecla-pattern				Yellow species, nastes-pattern			
C. chrysotheme	5	1.350	1.89				
C. croceus, Europe	10	1.403	1.90	C. alpherahyi	1	1.436	2.02
-"- , Asia	11	1.429	1.89	C. christophi	1	1.369	1.86
C. eogene	8	1.368	1.87				
C. heos	12	1.474	1.99	C. cocandica	2	1.326	1.85
C. remanovi	2	1.446	1.91	C. phicomone	24	1.374	1.88
C. standingeri	6	1.395	1.83	C. sieversi	1	1.405	1.93
C. thisoa	2	1.417	1.90	C. sifanica	1	1.326	1.90
C. wiscotti	9	1.431	1.93				
C. viluensis	7	---	1.90				

Table 2. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, in some Colias species with a broad superuncus. Logarithmic scale.

and Sredne Kolymsk.. The latter specimens all have a slender and strongly bent superuncus of the *hecla*-type, while all specimens of *viluiensis* have a straighter and broader superuncus. There is no overlap in any of the two characters; in the "angle-character" the gap is very wide.

In *Colias nastes* from Asia there is no similar correlation between the breadth and the shape of the superuncus. Among the 41 specimens investigated the coefficient of correlation is +0.093 which is far below significance ($0.8 > P > 0.7$).

Conditions are thus quite different in northern Asia as regards the *nastes*- and *hecla*-series of forms. In the *nastes*-series clines including characters of the genitalia reach the Amur area, Transbaikal, the Sayan Mts, and the Altai, and forms intermediate between arctic and Central Asiatic ones are present in North Western China and in the mountains of Central Europe. In the orange series of forms an overlap of a northern and a southern species is present between 65°-68° n. latitude and no intermediates have yet been found between these species.

Number of teeth near apex of aedeagus. In many groups of insects the number, shape, and position of the aedeagal teeth serve as good evidence to distinguish species. In the *Colias* species all the teeth are small, of a rather similar shape, situated near the apex. Variation in number is strong even within subspecies when compared with the differences occurring between species. Thus this character is without signifiance for the determination of individuals. A closer investigation of a material belonging to the group of species with a slender super-

	n	$M_{\log x}$	$M_{\log y}$
C. aurorina	6	1.449	1.80
C. sagartia	5	1.437	1.76
C. australis	8	1.384	1.74
C. hyale	27	1.373	1.79
C. erate	13	1.387	1.94
C. myrmidone	7	1.425	1.95
C. cunninghami	2	1.367	2.01
C. vautieri	2	1.327	1.83
P. imperialis	1	1.356	2.05

Table 3. Wing length (x), in mm, and breadth of superuncus (y), in an arbitrary scale, in some Colias species.

uncus, however, revealed some slight specific differences in the average number of teeth (cf. Table 5). The results of this investigation are:

C. nastes has on an average fewer teeth than *C. hecla* from the same locality (Scandinavian material $t = 2.45$; $0.02 > P > 0.01$, American material not differing significantly. There is a certain tendency of parallelism, both species having a lower number of teeth in Scandinavia than in North America. This tendency is not significant in any of the species, however. *C. palaeno* and *interior* both have a low number of teeth, while the number is fairly high in *C. meadi, philodice,* and *eurytheme.*

SPECIAL PART

The genus *Colias* may be parted in two genera: *Protocolias* (type *imperialis* Btlr.) and *Colias,* the latter in turn in two subgenera *Mesocolias* (type *vautieri* Guér.) and *Colias.* The descriptions of the genera, the subgenera and their various species may be given most easily in the form of a key.

1. Small or medium-sized, orange butterflies with broad (0.40-0.45 mm) or very broad (0.5 mm), straight superunci. Superficial scales —if present—yellow and black, broad and flattened in the distal part. Apex of aedeogus without teeth.
Genus *Protocolias* and subgenus *Mesocolias* 2.

1'. Small to big, yellow, greenish or orange species with broad to slender (0.32 mm) superunci. Superficial scales in the black margin—if present—yellow, pointed, hairlike or broader. A number of teeth at apex of aedeagus
Subgenus *Colias* 3.

2. Superuncus very broad and triangular. Pseudouncus short. Clasperhead with elongated tooth. Middle part of the clasper with a marked prong. Ventral arm of aedeagus broader in the distal end. Black and yellow superficial scales present.
Protocolias imperialis Btlr. (Pl. I:1)

2'. Superuncus broad. Tooth of clasperhead slightly bent upwards. Ventral lobe (v.l.) of inner side of the clasper (Klots 1929 a) more marked than in any other species of the genus. Distal part of ventral arm of aedeagus showing characteristic shape. Superficial scales absent.
Colias (*Mesocolias*) *vautieri* Guér. (Pl. I:2,3)

2". Superuncus very broad, genitalia small, claspers short (1.0-1.1 mm) but broad (0.6 mm). Distal part of ventral arm of aedeagus not broader than the proximal one. Superficial scales absent.
Colias (*Mesocolias*) *cunninghami* Btlr. (pl. I:4).

3. Claspers caudally with a marked prong directed medially. Superuncus straight and fairly slender.
C. hyale L. (pl. I:5) and *australis* Ver.

3'. Claspers without any marked prong ..... 4.

4. Claspers pointed in the middle part of the caudal edge (most easily seen from behind) ..... 5.

4'. Claspers not pointed in the middle part of the caudal edge 6.

5. Superuncus straight, on an average 0.40-0.45 mm broad
C. erate Esp., *C. myrmidone* Esp. (Pl. I:6).

5'. Superuncus usually markedly bent downwards, 0.30-0.35 mm broad.
C. sagartia Led. (Pl. I:7) *C. aurorina* H. Sch. (Pl. I:8).

6. Superuncus on an average less than 0.32 mm broad (cf. text fig. 3) usually strongly bent downwards (cf. Table 4) ..... 7.

6'. Superuncus on an average broader than 0.35 mm, usually straight ..... 13.

7. Superuncus only slightly bent downwards ..... 8.

7'. Superuncus strongly bent downwards ..... 9.

8. Superuncus in caudal view blunt-ended as in species with a broad superuncus. Inner side of clasper of *hecla*-type (cf. Pl. II:34)
C. montium Oberth. (Pl. I:9, 10).

8'. Superuncus in caudal view pointed. Inner side of clasper with well developed ventral lobe and ridged from its dorsal edge dorsocaudally towards the caudal part of the clasper (Fig. 14, 15)
C. interior Scudd. (Pl. I: 11-13, II: 14, 15).

9. Ridge from dorsal edge of ventral lobe towards caudal part of the clasper present as in *C. interior*. Ventral lobe less well developed than in *C. interior* (cf. Fig. 16). Caudal edge of clasper often strongly bent inwards (most easily seen in caudal view).
C. palaeno L. (Pl. II:16-25).
C. christina Edw. (Pl. II:26-28).
C. palaeno: is most variable in all characters investigated except the breadth of superuncus (cf. the figures). One specimen from Abisko (42 specimens studied) completely lacks the ridge on the inner side of the clasper. Hence it cannot with certainty be separated from *C. nastes* or *hecla*. The limited material of *C. christina* appeared rather close to some specimens of *palaeno*, though it might be possible to separate the two species after examining a greater material.

9'. The caudal edge of the valva less strongly bent inwards ventrally. Inner side of clasper reminding of *hecla*-type (cf. fig. 34) ..... 10.

10. Clasper (in lateral view) broadest rather ventrally ..... 11.

10'. Clasper broadest in the middle part ..... 12.

11. Aedeagus on an average with a higher number of teeth at the distal end ..... *C. hecla* Lef. (Pl. II:29-39).

Species, Population	Angle													Frequency of superuncus broken
	5–14	15–24	25–34	35–44	45–54	55–64	65–74	75–84	85–94	95–104	105–114	M	
Pop. of Table 1.													
C. hecla, Scand. Mts.						1	3	3	4	2		82	7/50
" , N. America				1	1	1	3		2			68	
C. hyperborea									3	1		93	
C. meadi					1			1	3	2	1	89	
C. eurytheme						1		2	2		1	85	7/17
C. palaeno, Scand. Mts.							2	1	4	1		85	14/56
" , Europe		1			1	5	4	3	4			69	14/56
" , Asia				1		1	1	1	2			72	14/56
" , N. America					1	4	2	1	2			69	14/56
C. interior [christina]			6	2	3							36	1/12
C. nastes, Scand. Mts.					2	1	3	6	8	1		80	4/25
" , Asia					2	2	1	4	17	4		85	7/41
" , N. America						1	1	1	1			75	
C. philodice							1	3	2	1		84	4/11
C. berylla				3								40	2/9
Pop. of Table 2.													
C. chrysotheme		2		1		2						40	
C. croceus, Europe		2	1									27	2/12
C. eogene		1	1		2	1						42	

11'. Aedeagus on an average with a lower number of teeth. Very similar to *C. hecla* .....*C. nastes* Bdv. (Pl. III:35-38).

12. Bigger, superuncus broader .....*C. eurytheme* Bdv. (Pl. III:39, 40).
C. philodice Gdt. (Pl. III:41).

12'. Smaller, superuncus slenderer. ....*C. meadi* Edw. (Pl. III:42, 43).

13. Superuncus bent downwards .....*C. phicomone* Esp. (Pl. III:44).

14. Superuncus diverging, very broad near the distal end. Clasper (in lateral view) broadest ventrally. ....*C. croceus* Fourcr. (Pl. III:45).

14'. Superuncus often with parallel or converging edges or clasper broadest in the middle part .....15.

15. Clasperhead more strongly marked, tooth strongly developed. Ventral arm of aedeagus broad in the distal part.
C. wiscotti Stgr. (Pl. III:46, 47)

C. marcopolo Gr. Grsh. probably also belongs here. No material has been available for investigation. Professor Sheljuzhko informs

C. heos		2	1	1	3	1															40	2/10	
C. romanovi			1																		30		
C. staudingeri			3																		30	2/6	
C. thisoa					2																50		
C. wiscotti		1	3	2	1	1															29		
C. viluensis			2	3	1																28	1/7	
C. alpherakyi		1																			10		
C. christophi				1																	30		
C. cocandica				2																	30		
C. phicomone					2	3	2	1	4	4											69	2/24	
C. sieversi		1																			20		
C. sifanica				1																	30		
Pop. of Table 3.																							
C. aurorina					2				2	1											66		
C. sagartia		1		1			1		2												58		
C. australis				3	1			1													38	3/8	
C. hyale		2		2		2	2														40	4/30	
C. erate		1		1																	20	2/15	
C. myrmidone			1	1			1														37		
C. cunninghami			1																		20		
C. wautieri			1																		25	1/3	
P. imperialis		1																			10		

Table 4. Angle (in degrees) of distal part of superuncus to dorsal edge of proximal part of VIIIth tergum.

that Avinov and Kusnezov both place *marcopolo* together with *wiscotti*, the latter as a subspecies. According to Sheljuzhko both forms fly together in the Pamir area and are probably different species in spite of a great similarity in the genitalia.

15'. Clasper head less strongly marked .....16.

16. A number of species remain which due to lack of sufficient material and/or great similarity could not be separated from each other:

Yellow species with *nastes*-pattern: *C. alpherakyi* Stgr. (Pl. III:48), *C. christophi* Gr.-Grsh. (Pl. IV:49), *C. cocandica* Ersch. (Pl. IV:50) (Specimen figured with triangular saccus; in a second specimen investigated the saccus is rounded as in all other species), *C. sieversi* Gr.-Grsh. (Pl. IV:51), *C. sifanica* Gr. Grsh. (Pl. IV:52). These Central Asiatic species together with *C. nastes, phicomone, montium* and others form one or—most probably—two polytypic species.

	n	2	3	4	5	6	7	8	9	10	11	12	M
C. hecla, N. Am.	8					5	1	2					6.6
" , Greenl.	3			1	1	1							5.0
" , Scand.	30			2	7	9	8	4					6.2
C. meadi	10					4	1	3	1			1	7.6
C. eurytheme	12				3	3	5		1				6.4
C. palaeno, N. Am.	10		1	1	5	2		1					5.2
" , Asia	8		1		1	6							5.5
" , Estonia	8		1		3		2	1	1				6.1
" , Scand.	21	1	2	7	2	3	1	3	1	1			5.4
C. interior	11			3	4	2	2						5.3
C. christina	1					1							6
C. nastes, N. Am.	6				1	4		1					6.2
" , Asia	5				1	3	1						6.0
" , Scand.	23		1	4	8	5	5						5.4
C. philodice	5				1	2	1				1		7.0

Table 5. Number of teeth near the apex of the aedeagus of Colias species with a slender superuncus.

Orange species with *hecla*-pattern: *C. chrysotheme* Esp. (Pl. IV:53), *C. eogene* Fldr. (Pl. IV:54, 55), *C. staudingeri* Alph. (Pl. IV:56), *C. thisoa* Mén. (Pl. IV:57), *C. viluiensis* Men., and *C. heos* (Pl. IV:58, 59). As in the previous group it is uncertain whether all these forms deserve each a specific status.

Orange species with *nastes*-pattern: *C. romanovi* Gr. Grsh. (Pl. IV:60).

This enumeration of *Colias* species is not complete.

DISCUSSION

The key given above does not show the phylogenetic relationships. These are, due to extensive introgressive hybridization, very difficult to find out. Suppose species A is closest related to the allopatric species B which has given rise to species C sympatric to A. Due to the introgressions A → C or C → A it is then possible that A and C are more similar in several characters than A-B or B-C. However, some characteristics, as for instance those on which the isolation between A and C depend, are likely to be of maximum difference in the case A-C.

Among the *Colias*-species investigated there exists a number of pairs of species within which the male genitalia are very similar: *C. eurytheme-philodice; C. hecla-nastes; C. aurorina-sagartia; C. myrmidone-erate; C. hyale-australis* and probably also *C. palaeno-christina* and *C. wiscotti-marcopolo*. Introgression has among these been established between *C. eurytheme-philodice* (Hovanitz 1949 a, b) and between *C. hecla* and *nastes*. Hybridization has been suggested between *C. sagartia* and *aurorina* (Lederer 1941). It is possible that pairs of a similar kind are present in Central Asia among the species figured from number

48 to number 58. Lederer (1941) mentions, among other suspected hybrids, specimens which have been supposed to be hybrids between *C. eogene* and *cocandica.* A number of species with different genitalia have been seen in copula (Lederer l.c.): *hyale* x *myrmidone, hyale* x *croceus, hyale* x *erate, croceus* x *erate,* and *hyale* x *phicomone.* The last cross gave rise to some larvae which died before the pupation. All these species have markedly different genitalia and are probably not very closely related. It therefore seems uncertain whether hybridization in these cases can give rise to introgression. If introgression occurs it must be possible to observe this fact also on the genitalia.

In all the pairs of sibling species first mentioned (*eurytheme-philodice* etc.), except *hyale-australis* and *palaeno-christina,* colors, and in most cases also patterns, are different. The first species is usually orange with a *hecla*-pattern, the second yellow with a *nastes*-pattern. Only *C. sagartia* has in addition a blue pigment which is present in some individuals of its orange sibling *aurorina.*

The common occurrence of differences in color and pattern between sibling species suggests that these colors are integrating part of the isolating mechanisms within the pairs. Sexual isolation of this kind has in the pair *Pieris napi-bryoniae* been established by Petersen, Tornblom and Bodin (1952). Males of both species are attracted by the white color of the *P. napi* female. The yellow female of *bryoniae* attracts the males solely by means of movements and odors. No releasing effect of any of the types of pattern was obtained neither in these pierids nor in similar experiments with the Silverwashed Fritillary (*A. paphia* L.) (Magnus 1954). Different color but probably not different pattern may therefore play a role for the sexual isolation between *Colias* species.

The geographical distribution of some subdivisions of the genus Colias may also be discussed. *Protocolias* and *Mesocolias* are entirely South American. The species of the subgenus *Colias* with a broad superuncus are all Palearctic, one group having penetrated even into the Ethiopian region. *Colias* with a slender superuncus are mainly distributed in North America and the northern Palearctic, only a few living further south in the latter region.

The distribution of the groups is to a great extent certainly the result of an evolution within different areas. It does not seem established that palearctic *Colias* have evolved from South American forms. They may as well have developed from primitive *Colias* in some other part of the world where they are now extinct.

The evolution of the superuncus. Among the two characteristics of the *Colias* genitalia, the superuncus and the pseudouncus, the latter is present in the genus *Anteos* as well as in *Catopsilia* and *Colias* (Klots 1929 a, b, Drosihn 1933). The superuncus, on the other hand, is very small and triangular in the *Anteos* species investigated (*menippe, clorinde,* Plate IV, figs. 61, 62) covering only the pseudouncus and the basal part of the uncus. A similar, though bigger superuncus is found in *Protocolias imperialis* and the genus *Phoebis* (Drosihn 1933). In

the latter genus no pseudouncus is present. The *Catopsilia* and *Aphrissa* species have broad, straight and diverging superunci (cf. Plate IV, figs. 63, 64 and Drosihn 1933), rather similar to those of some *Colias* species. The triangular shape of the superuncus is probably primitive, as this shape is present in *Anteos* where the superuncus is comparatively small.

The superuncus has in the genus *Colias* (and probably also in *Catopsilia* and *Aphrissa*) taken over the function of the uncus of many other Lepidoptera (cf. Lorkovic 1947) to assist medially and dorsally in holding the female body during the copulation. The superuncus and the pseudouncus probably developed to support the uncus dorsally. As the superuncus became larger, it was placed directly against the female body, and thus the uncus instead changed to support the superuncus.

It has been suggested, for instance by Verity (1947), that *Colias* have developed from the Old World *Catopsilias*. The presence of the very primitive *Protocolias* with a triangular superuncus, a short pseudouncus, and the middle part of the clasper with a prong, makes this assumption rather unlikely. The triangular superuncus may be considered as a very pronouncedly convergent one (cf. fig. 2). The more or less parallel or divergent superunci of *Colias, Catopsilia* and *Aphrissa* may have evolved by means of parallel evolution towards more uncus-like conditions as discussed below in the case of *Colias*.

The *Catopsilias* and most *Colias* species have broad, straight, and unpointed superunci, characteristics which therefore may be considered primitive compared with those of *C. hecla, nastes* and *palaeno*. A similiar result is arrived at, if the problem is approached from another direction. As already mentioned the superuncus has in the genus *Colias* taken over the function of the uncus. The latter has had its function during so much longer a time that it may give a certain indication of what shape is most apt to give an optimal function. The uncus is slender, pointed, and rather straight. In the two first of these characteristics the uncus corresponds to the superuncus of the *hecla-nastes-palaeno*-type. Only it is even more pronounced then. The shape of the uncus on the other hand, is straighter in lateral view. The basal part of the superuncus is, however, situated more dorsally than the same part of the uncus (cf. textfig. 13). Only if the superuncus is bent downwards, it can be placed against the female body in the same place as the uncus of other Pierids.

The evolution of the superuncus thus seems to have converged with that of the uncus. There is, however, still a marked difference in shape between these two organs and for different reasons it is not likely that the convergence will become complete ever. As already mentioned the situation of the two organs is different. The pressure of the superuncus is supported by that of the uncus and probably also by that of the pseudouncus, and finally the claspers are in the genus *Colias* not built as in other genera.

SUMMARY

The male genitalia of a number of *Colias* species have been described. The genus is divided into one new genus and two subgenera of the genus *Colias*: The South American genus *Protocolias* (type *imperialis* Btlr.) and subgenus *Mesocolias* (type *vautieri* Guér.) and the mainly Holarctic subgenus *Colias*. The latter can be divided into a palearctic group with a broad straight superuncus and a nearctic and northern palearctic group with a slender superuncus which is bent downwards. Transitions between these two groups exist within the supraspecies *C. nastes*.

The evolution of the superuncus from a small beginning, as at present in the genus *Anteos*, via the broad superunci of the *Catopsilias* and some *Colias* into a slender superuncus has been discussed.

Several pairs of *Colias* species with identical or very similar genitalia exist. It is suggested that the similarity is combined with introgression. Several of the pairs include species of different colors. These colors may serve to isolate the species sexually from each other.

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PLATES

a. lateral view
b. superuncus, dorsal view
c. caudal view
d. aedeagus, ventral or dorsal view
e. " , distal end in lateral view
f. clasper from inner side
g. saccus in ventral view
u. uncus
v.l. ventral lobe of the inner side of the clasper (Klots 1929 a)

PLATE I.

Fig. 1. *P. imperialis* (wrongly labelled Honolulu)
Fig. 2. *C. vautieri*, Ensenada
Fig. 3. *C. vautieri*, Ensenada
Fig. 4. *C. cunninghami*, Junin, Peru
Fig. 5. *C. hyale*, Oland, Sweden
Fig. 6. *C. myrmidone*, Germany
Fig. 7. *C. sagartia*, N.E. Persia
Fig. 8. *C. aurorina*, Armenia
Fig. 9. *C. montium*, Tatsienlou, Tibet
Fig. 10. *C. montium*, S. Kansu, China
Fig. 11. *C. interior*, Montreal, Canada
Fig. 12, 13. *C. interior*, Alaska Highway, mile 126, Beatton R. area, B.C.

PLATE II.

Fig. 14. *C. interior*, Alaska Highway, mile 90, Beatton R. area, B.C.
Fig. 15. *C. interior*, Alaska Highway, mile 90, Beatton R. area, B.C.
Fig. 16. *C. palaeno*, Alaska Highway, mile 450, Toal River, B.C.
Fig. 17. *C. palaeno*, Bjurfors, Sweden
Fig. 18. *C. palaeno*, Sweden
Fig. 19, 20. *C. palaeno*, Smaland, Sweden
Fig. 21. *C. palaeno*, Abisko, Sweden
Fig. 22, 23. *C. palaeno*, 10 miles South Burwash Landing, Y.T.
Fig. 24, 25. *C. palaeno*, Sweden
Fig. 26. *C. christina*, America borealis
Fig. 27. *C. christina*, Rocky Mts.
Fig. 28. *C. christina*, Am. bor.
Fig. 29. *C. hecla*, Nr. Haines Junction, Y.T., up Summit Cr. 6000'-7000' el.
Fig. 30. *C. hecla*, Bog. nr. Johnson's Crossing, Y. T.
Fig. 31. *C. hecla*, Dudinska, Siberia
Fig. 32. *C. hecla*, Sweden
Fig. 33. *C. hecla*, Kvikkjokk, Sweden
Fig. 34. *C. hecla*, 20 miles South Burwash Landing, Y. T.

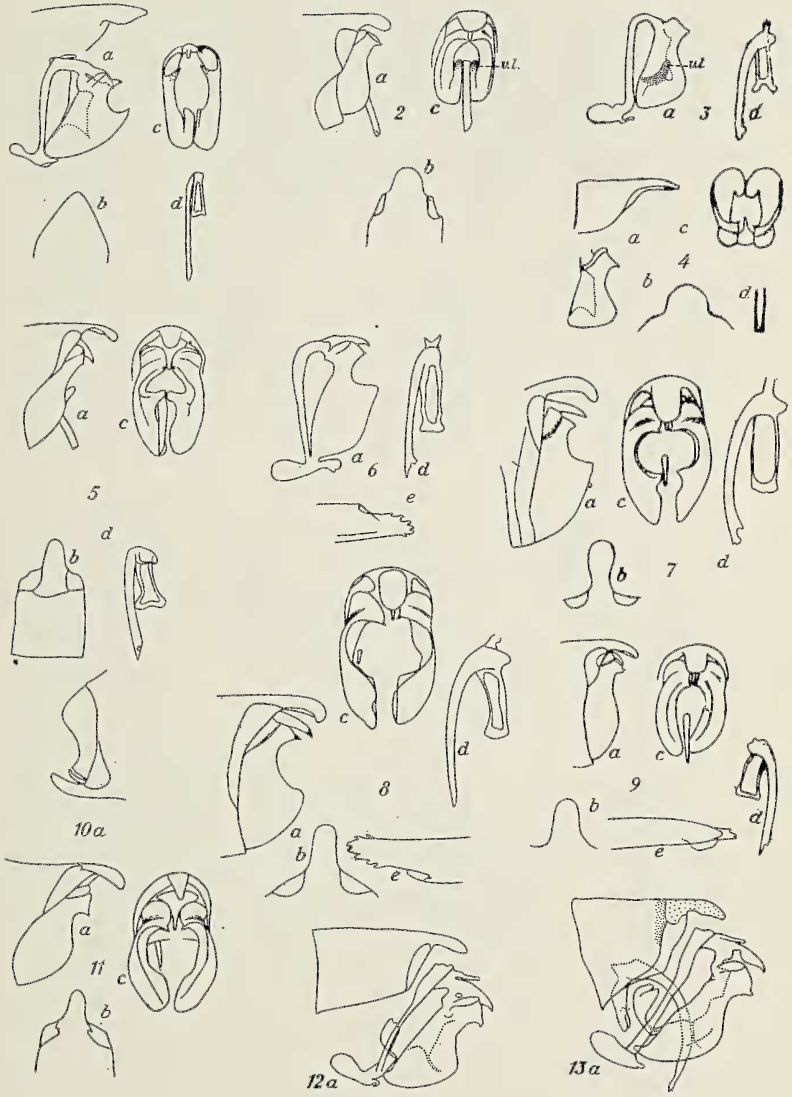
PLATE III.

Fig. 35. *C. nastes*, Nr Haines Junction, Y. T., up Summit Creek, 6000'-7000' el.
Fig. 36. *C. nastes*, Mt. Atabaska, Jasper N.P., Alberta, 7000'-8000' el.
Fig. 37, 38. *C. nastes*, Kvikkjokk, Swedish Lapland
Fig. 39. *C. eurytheme*, Texas
Fig. 40. *C. eurytheme*, Minnesota, U.S.A.
Fig. 41. *C. philodice*, Amer. bor.
Fig. 42, 43. *C. meadi*, Bow Pass, Jasper N. P., Alberta
Fig. 44. *C. phicomone*, Alps
Fig. 45. *C. croceus*, Tirol, Austria
Fig. 46. *C. wiscotti*, Turkestan
Fig. 47. *C. wiscotti separata*, Turkestan
Fig. 48. *C. alpherakyi*, Turkestan

PLATE IV.

Fig. 49. *C. christophi*, Turkestan
Fig. 50. *C. cocandica*, Turkestan
Fig. 51. *C. sieversi*, Turkestan
Fig. 52. *C. sifanica*
Fig. 53. *C. chrysotheme*
Fig. 54. *C. eogene*, Kisil Fast area
Fig. 55. *C. eogene*
Fig. 56. *C. staudingeri*, *Tian Shan*, Fu-Shu-Shan
Fig. 57. *C. thisoa*
Fig. 58. *C. heos*, N. Mongolia, long. 100°-110°, lat. 45°-50°
Fig. 59. *C. heos vespera*, S. Kansu, China
Fig. 60. *C. romanovi*, Turkestan
Fig. 61. *Anteos menippe*, Mattogrosso
Fig. 62. *A. clorinde*, Valles, Mex.
Fig. 63. *Catopsilia florella*, Syria
Fig. 64. *C. grandidieri*, Madagascar

PLATE I



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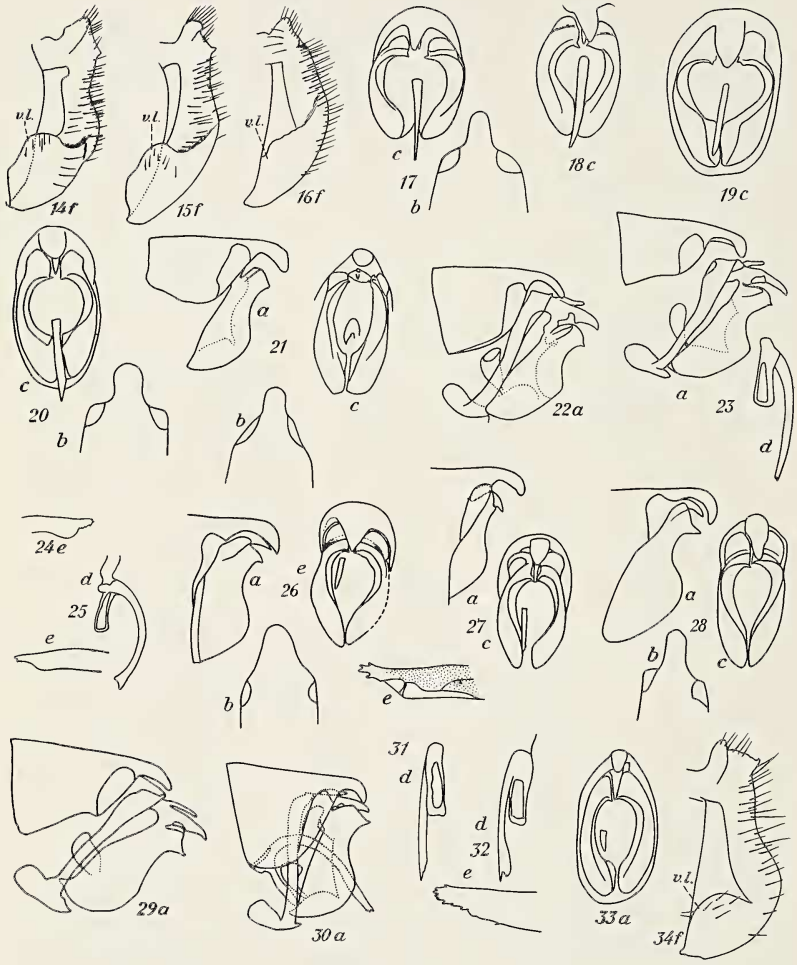
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PLATE III

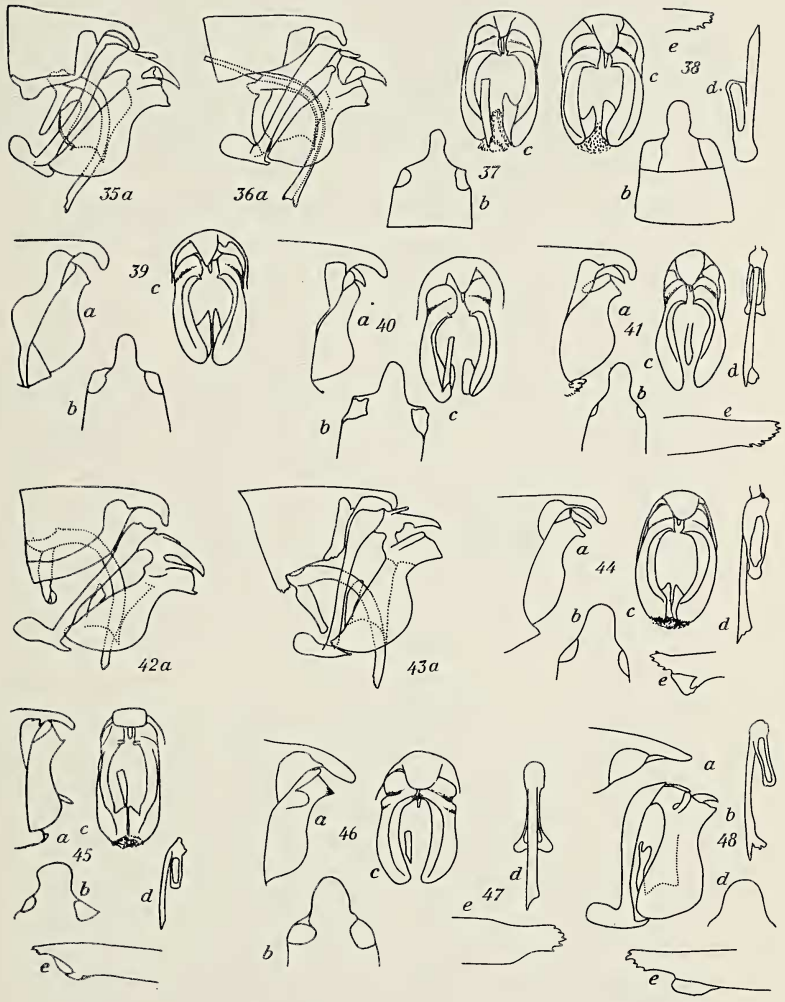

PLATE IV